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E-CHAPTER FROM THIS BOOK



Restoring degraded grasslands

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1 Introduction

Grasslands are complex ecosystems comprising numerous biotic and abiotic components. The biotic components are the herbaceous grass and forb plants, soil organisms and grazing graminivores which have biological and physiological requirements. The abiotic components include radiant energy from sunlight; the essential major elements of carbon, hydrogen, nitrogen and oxygen, and the minor essential elements of macro- and micro-minerals required by living organisms. The major elements and some of the minor elements have biogeochemical cycles which transform the elements between organic and inorganic forms. Grassland ecosystems are therefore functioning units of co-acting biotic organisms interacting with the abiotic components and environmental factors (Manske 2014c). Grass plants, soil microorganisms and large graminivores have developed complex symbiotic relationships. The grazing graminivores depend on grass plants for nutritious forage; grass plants in turn depend on rhizosphere organisms for the mineralisation of essential elements (primarily nitrogen) from the soil organic matter; rhizosphere organisms depend on grass plants for energy in the form of the short carbon chains released by grass plants into the rhizosphere following partial defoliation by grazing graminivores. The management of grassland ecosystems must therefore meet the biological and physiological requirements

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of the plants, soil organisms and graminivores; stimulate internal plant mechanisms; and enhance the rhizosphere organism biomass and the ecosystem biogeochemical processes that cycle essential elements (Manske 2014c).

Grassland ecosystems degrade when management causes the loss of essential elements to be greater than the capture of replacement essential elements. Conversely, grassland ecosystems aggrade when they are managed so as to make the capture of essential elements greater than the losses (McGill and Cole 1981). A large biomass of soil microbes is required to aggrade grassland ecosystems (Coleman et al. 1983; Schimel, Coleman and Horton 1985; Cheng and Johnson 1998). The soil microorganism biomass can be increased through biologically effective grazing management. Traditional management of grasslands causes a diminution of the functionality of internal grass plant mechanisms and ecosystem biogeochemical processes, resulting in degradation. Therefore, restoration of degraded grassland ecosystems requires returning the primary grass mechanisms and ecosystem processes to potential functioning levels. As an initial step, the rhizosphere organism biomass must be raised to increase the mineralisation of nitrogen and other essential elements. Rhizosphere organisms are limited by accessing energy in the form of short carbon chains. Carbon energy can be released from grass lead tillers through the roots into the rhizosphere by removal of 25–33% of the above-ground leaf biomass by large grazing graminivores when the lead tillers are at the phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage during early June to mid-July (Manske 1999, 2011b, 2014c). Depending on the degree of degradation of the grassland, three to five or more growing seasons are required to increase the rhizosphere organism biomass to levels capable of mineralising a threshold level of 112 kg/ha or greater of available mineral nitrogen. Research has shown that full activation of internal grass plant mechanisms requires mineral nitrogen to be available at this level. It also requires available carbon fixed through photosynthesis from 67 to 75% of the leaf area of pre-defoliated lead tillers before the flower stage, and from 50% of the leaf area after the flower stage (Manske 2010a,b). An increase in available essential elements permits the grass tillers to synthesise increasing quantities of carbohydrates, proteins and nucleic acids to accelerate growth rates of replacement leaves and shoots, increase photosynthetic capacity of the remaining mature leaves, increase secondary tiller development from axillary buds, enhance the competitiveness of nutrient resource uptake and improve water use efficiency. The combination of increased ecosystem biogeochemical processes and improved functioning of the internal grass plant mechanisms results in increases in grass herbage production and in plant density (basal cover) of the desirable native grass species. Changes in the above-ground vegetation lag behind changes in the soil microorganism biomass and activity when a grassland ecosystem is degrading and also when it is aggrading.

This chapter examines the inter-relationship of species, microbial activity, nutrients and environmental factors in restoring and maintaining the health, sustainability and productivity of grasslands, with particular emphasis on the ecosystem of the Northern Plains of North America. The information presented here was synthesised from research conducted in the Northern Plains and should be directly applicable to all intact grassland regions where perennial grass plants reproduce vegetatively and the plants subsist from growing season to growing season in a low-activity dormancy state when soils are frozen. The Northern Plains ecosystem is part of the North American Interior Plains physiographic region that extends from the foot of the Rocky Mountains eastwards to the Canadian Shield and Appalachian Provinces, and in the north extends from the Athabasca River on the Alberta Plateau southwards to the North Platte-Platte-Missouri River Valleys. The

native vegetation was primarily grasslands which have been separated into four types arranged in north–south zones based on the stature of the major grass species on the silty ecological sites. The native vegetation types from west to east are: short grass, mixed grass, transition (or Eastern mixed grass), and tall grass prairies. Each of these vegetation types has been defined by soil temperature and soil moisture regimes. The two soil temperature regimes are based on mean annual soil temperature: in the north by $<8^{\circ}\text{C}$ (Frigid) and in the south by $>8^{\circ}\text{C}$ (Mesic). The separation between north and south soil temperature regimes is demarcated by a wide belt that extends eastwards along the north border of Wyoming and continues through South Dakota to the boundary of the Oak Forest in western Minnesota. The four soil moisture regimes are based on the mean annual precipitation and the mean length of time the soil is dry during a growing season. Most of the precipitation (75–85%) occurs during the growing season. Precipitation rates increase from west to east. In the north, the range is from 305 mm in the west to 610 mm in the east. In the south, the range is from 356 mm in the west to 813 mm in the east. The number of days the soil is dry during a growing season decreases from west to east. The resulting four soil moisture regimes are: arid (Aridic), semi-arid (Ustic), sub-humid (Udic) and humid (Perudic). Soils of the short grass prairie support vegetation of short grasses with some mid grasses in the north and of short grasses in the south. The major species are: blue grama (*Bouteloua gracilis*), needle and thread (*Hesperostipa comata*), and western wheatgrass (*Pascopyrum smithii*). Soils of the mixed grass prairie support vegetation of mid and short grasses in the north and of mid and short grasses with tall grasses on the lower slopes in the south. The major species are: western wheatgrass, needle and thread, and blue grama. Soils of the transition prairie support vegetation of mid grasses and some tall grasses in the north and of mid and tall grasses in the south. The major species are: western wheatgrass, little bluestem (*Schizachyrium scoparium*), and needle and thread. Soils of the tall grass prairie support vegetation of tall grasses in the north and south. The major species are: big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*) and porcupine grass (*Hesperostipa spartea*) (Manske 2008d). Within each of the four prairie types there are differences in plant community structure resulting from variations in the physical, chemical and/or biological characteristics of the soils.

The fertile soils of the tall grass and transition prairies are good for the production of agronomic crops, and much of these native grasslands have been ploughed. Agricultural practice with regard to intact (non-ploughed) grasslands in the Northern Plains has traditionally involved the removal of a portion of above-ground herbage as forage for domesticated livestock. The degree of annual use and level of deterioration are inversely related to the level of managerial land stewardship ethics, and degradation of grassland primarily results from a failure to incorporate into management systems the concept of grasslands as fully functioning ecosystems.

2 Grass plant responses to defoliation

The key factor in meeting grass plant biological requirements is the correct timing of partial defoliation. The effects of defoliation are not simply the removal of herbage from grass plants: foliage removal disrupts plant growth and photosynthesis, and defoliation also affects physiological mechanisms in all parts of the plant (Langer 1956, 1963, 1972). It alters the plant community microclimate by changing light transmission, moisture relations and

temperature (Briske and Richards 1994, 1995), and it changes the soil environment, thereby affecting soil organism activity and ecosystem biogeochemical processes (Manske 2000a, 2011b). Internal plant mechanisms help grass tillers to withstand and recover from partial defoliation by grazing. The primary internal mechanisms are: compensatory physiological mechanisms (McNaughton 1979, 1983; Briske 1991); vegetative reproduction by tillering (Mueller and Richards 1986; Richards et al. 1988; Murphy and Briske 1992; Briske and Richards 1994, 1995); and nutrient resource uptake (Crider 1955; Li and Wilson 1998; Kochy and Wilson 2000; Peltzer and Kochy 2001). In addition, the level of available soil mineral nitrogen has a strong effect on grasses' response to defoliation by influencing compensatory physiological mechanisms and the functionality of vegetative reproduction. These factors are discussed in the following sections.

2.1 Compensatory physiological mechanisms

Compensatory physiological mechanisms give grass plants the capability to replace lost leaf and shoot biomass following grazing by increasing meristematic tissue activity and photosynthetic capacity, and by altering the allocation of carbon and nitrogen. Fully activated mechanisms can produce replacement foliage at 140% of the weight removed during grazing (Manske 2000b, 2010a,b, 2014a,b). The growth rates of replacement leaves and shoots increase after partial defoliation by grazing, and enhanced activity of the meristematic tissue produces larger leaves with greater mass (Langer 1972; Briske and Richards 1995). Developing leaf primordia not fully expanded at the time of defoliation show increased growth rates and tend to grow larger than leaves on undefoliated tillers (Langer 1972). Partially defoliated tillers increase the photosynthetic rates of the remaining mature leaves and rejuvenated portions of older leaves which are not completely senescent (Atkinson 1986; Briske and Richards 1995). Changes in cytokinin levels and other signals produced as a result of the increase in the root–shoot ratio may rejuvenate the photosynthetic apparatus, inhibit or reduce the rate of senescence and increase the lifespan and leaf mass of the remaining mature leaves (Briske and Richards 1995). The activation of compensatory physiological mechanisms after grass tillers are partially defoliated by grazing requires alternative sources of abundant carbon and nitrogen (Coyne et al. 1995). To achieve this the carbon fixed during current photosynthesis in the remaining mature leaf and shoot tissues, and in the rejuvenated portions of older leaves, is preferentially allocated to areas of active meristematic tissue (Ryle and Powell 1975; Richards and Caldwell 1985; Briske and Richards 1995; Coyne et al. 1995). The leaf area required to fix adequate quantities of carbon is 67–75% of the pre-defoliated leaf area (Manske 1999, 2011b, 2014c). Very little, if any, of the carbon and nitrogen stored in the root system is remobilised to support compensatory growth (Briske and Richards 1995). Pools of mobilisable nitrogen in the shoot tissue are reduced following partial defoliation, and this increases preferential use of mineral nitrogen available in the media around the roots (Millard et al. 1990, Ourry et al. 1990). This available soil mineral nitrogen is converted from soil organic nitrogen by active rhizosphere organisms, absorbed through the roots and moved to areas of active meristematic tissue.

2.2 Vegetative reproduction by tillering

Vegetative secondary tillers are shoots which develop on lead tillers from the growth of axillary buds by the process of tillering (Hyder 1974; Dahl and Hyder 1977; Dahl 1995).

Meristematic activity in axillary buds and the subsequent development of vegetative tillers are regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin interference with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material during the vegetative growth stages temporarily reduces the production of auxin (Briske and Richards 1994). The abrupt reduction of this hormone in the lead tiller allows for cytokinin synthesis or utilisation in multiple axillary buds, thus stimulating the development of vegetative secondary tillers (Murphy and Briske 1992; Briske and Richards 1994). If no defoliation occurs before anthesis, the lead tiller will continue to hormonally inhibit the development of the secondary tiller from axillary buds. The production of auxin declines gradually as the lead tiller reaches the flower stage. The natural reduction of auxin in the lead tiller usually permits only one secondary tiller to develop. This developing secondary tiller produces auxin which suppresses the development of additional axillary buds (Briske and Richards 1995). Vegetative tiller growth is the dominant form of reproduction in semi-arid and mesic grasslands, not sexual reproduction and the development of seedlings (Belsky 1992; Chapman and Peat 1992; Briske and Richards 1995; Chapman 1996; Manske 1999). Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely low in functioning grasslands, and their establishment occurs only during years of favourable moisture and temperature conditions (Wilson and Briske 1979; Briske and Richards 1995), in areas of reduced competition from vegetative tillers, and when resources are readily available to the growing seedling.

2.3 Nutrient resource uptake

The dominance of grass plants within a grassland community is related to their competitiveness in terms of nutrient and water resource uptake, but this can be compromised by poor management. For example, Crider (1955) found that grass tillers with 50% or more of the above-ground leaf material removed experienced reduced root growth, root respiration and root nutrient absorption, resulting in reduced functionality of these plants. Reduction of the active root biomass has been found to cause a diminution of grass plant health and vigour (Whitman 1974), leading to a loss of resource uptake efficiency and suppression of the competitiveness of grass plants in taking up mineral nitrogen, essential elements and soil water (Li and Wilson 1998; Kochy 1999; Kochy and Wilson 2000; Peltzer and Kochy 2001). The loss of active root length thus contributes to a reduction in rhizosphere biomass and a decline in ecosystem biogeochemical processes (Coleman et al. 1983; Klein et al. 1988). The nutrient resource uptake competitiveness of healthy grasses is able to suppress the expansion of shrubs and prevent successful establishment of grass, forb and shrub seedlings in grasslands (Peltzer and Kochy 2001). The grass growth form has competitive advantages for nutrient uptake over the shrub growth form (Kochy and Wilson 2000). The above-ground biomass of grasses consists primarily of productive photosynthetic leaves, resulting in high resource uptake efficiency. Grasses are good competitors for below-ground nutrient resources and are superior competitors for mineral nitrogen due to a high root-to-shoot ratio and the absence of woody stems to be maintained. The resource uptake efficiency of shrubs is greatly reduced because a large portion of the photosynthates is used to build and maintain their unproductive woody stems. However, taller woody stems make shrubs superior competitors for above-ground

sunlight resources (Kochy and Wilson 2000). Competition from healthy grasses for below-ground nutrient resources reduces the growth rates of shrub rhizomes and causes high mortality rates among young suckers (Li and Wilson 1998). Shrubs are able to compete for some of the below-ground resources only where the functionality of grass plants has been degraded by ineffective management. Following such reduction, the below-ground resources no longer consumed by the smaller, less vigorous degraded grasses are taken up by shrub plants, resulting in proportional increases in shrub biomass production (Kochy and Wilson 2000). With greater access to nutrient resources, shrub rhizome suckers are able to establish a faster growth rate and a higher survival rate (Li and Wilson 1998). The resulting greater shrub stem density increases competition for light, causing marked suppression of grasses (Kochy and Wilson 2000). Traditionally, the observation of increasing presence of woody shrubs and trees in degraded grasslands would have been attributed to fire suppression (Humphrey 1962; Stoddart, Smith and Box 1975; Wright and Bailey 1982).

2.4 Threshold level of soil mineral nitrogen

Total herbage biomass production in grassland ecosystems has been shown to increase when the quantity of available soil mineral nitrogen increases (Rogler and Lorenz 1957; Whitman 1957, 1963, 1976; Smika et al. 1965; Goetz 1969, 1975; Power and Alessi 1971; Lorenz and Rogler 1972; Taylor 1976; Wight and Black 1979). Grasslands in the Northern Plains which are managed with traditional grazing practices are notorious for their inhibitory deficiency in available soil mineral nitrogen (Goetz et al. 1978), and this leads to their observed low herbage production. In temperate grasslands, deficiencies of mineral nitrogen are more often a cause of limited herbage production than lack of water (Tilman 1990). However, greater quantities of available soil mineral nitrogen have been shown to improve soil water use efficiency in grassland plants (Smika et al. 1965; Wight and Black 1972; Whitman 1976, 1978). Using a proxy method, Wight and Black (1972) found that precipitation (water) use efficiency of grass plants improved when soil mineral nitrogen was available at threshold quantities of 112 kg/ha. The inhibitory effect of deficiencies of mineral nitrogen on grasslands caused herbage production per centimetre of received precipitation to decrease by almost 50% relative to that in grasslands above the threshold (Wight and Black, 1979). Manske (2010a,b) found that this threshold quantity of available mineral nitrogen was also critical for the functionality of vegetative reproduction and for compensatory physiological mechanisms in response to defoliation. Both these mechanisms function at high potential levels in grasslands having 112 kg/ha or greater available soil mineral nitrogen, and do not function (or function at extremely low levels) in those which have mineral nitrogen deficiencies (Manske 2009c, 2010a,b,c, 2011c,d).

3 Agronomic practices to increase soil nitrogen levels

Traditional grazing management practices are known to be antagonistic to rates of mineralisation of soil organic nitrogen, resulting in levels of available mineral nitrogen lower than the threshold quantity of 112 kg/ha (Wight and Black 1972). Previous research in the North American Northern Plains, aimed at developing strategies to increase the quantity of mineral nitrogen in grassland soils, did not incorporate grazing treatments, and instead concentrated on agronomic practices such as nitrogen fertilisation and

inter-seeding alfalfa. The application of nitrogen fertiliser to grasslands did not solve the complex problems related to the causes of low soil mineral nitrogen (Manske 2014d). It was found that nitrogen fertilisation of native grasslands caused a synchronisation of grass tiller growth stage development, resulting in a small increase in herbage biomass which later produced a high rate of leaf senescence and an early season decrease in forage nutritional quality compared to non-fertilised grasslands (Manske 2014d). It also caused a short-term shift in plant species composition, with an increase in mid cool season grasses (e.g. western wheatgrass) and a decrease in short warm season grasses (e.g. blue grama) (Manske 2014d). Initially, these changes were considered to be beneficial (Manske 2009d). However, close examination of the data showed that the costs of the additional herbage weight were excessive (Manske 2009b), and that the long-term disruptions of ecosystem biogeochemical processes were detrimental to desirable plant composition (Manske 2010c). The reduction of short warm season grasses caused a decrease in total live plant basal cover, thus exposing greater amounts of soil to higher levels of solar radiation and erosion (Goetz et al. 1978). These large areas of open space became ideal invasion sites for undesirable plants, resulting in a long-term plant species compositional shift towards a replacement community of domesticated and introduced mid cool season grasses, and in the removal of nearly all the native plant species (Manske 2009a, 2010c). Neither did the strategy of inter-seeding alfalfa into intact semi-arid grasslands solve the complex problems related to the causes of low soil mineral nitrogen (Manske 2005). The introduction of alfalfa increased demand on the existing low levels of soil mineral nitrogen because almost all of the alfalfa plants' nitrogen requirements had to be taken from the soil. The inter-seeded alfalfa plants had extremely low levels of nodulation of rhizobium bacteria on the roots and, consequently, almost no nitrogen fixation. The inoculated rhizobium had been consumed by the resident soil microbes before the alfalfa seedlings had grown sufficient root material to permit infection (Manske 2004b). The low amounts of mineral nitrogen available in the soil resulted in slower rates of growth and higher rates of mortality for the inter-seeded alfalfa plants than those for alfalfa plants solid-seeded into cropland (Manske 2005). In addition, the high water use of the inter-seeded alfalfa plants depleted soil water levels within a 1.5-m radius of each crown to an average of 35% below ambient soil water levels, causing drought stress conditions in the adjacent grass plants and, subsequently, further reducing grass herbage production (Manske 2004a, 2005). In summary, these agronomic strategies slowly stifled grass internal mechanisms and ecosystem biogeochemical processes to ineffectiveness. Grassland ecosystems should, therefore, be managed in accordance with sound ecological principles. These will be described in subsequent sections.

4 Effects of rhizosphere organisms on biogeochemical processes

The rhizosphere (Fig. 1) is the narrow zone of soil around the active roots of perennial grassland plants. In sustainable grassland systems the biogeochemical processes performed by rhizosphere microorganisms renew nutrient flow activities in the soil. Biogeochemical processes transform stored essential elements from organic forms into plant-usable inorganic forms. These processes capture replacement quantities of lost or removed major essential



Figure 1 Rhizosphere on western wheatgrass root.

elements of carbon, hydrogen, nitrogen and oxygen, with assistance from active live plants, and transform them into storage as organic forms for later use. They decompose complex unusable organic material into compounds and then into reusable essential elements (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995). The quantity of biogeochemical processes taking place in grassland ecosystems is dependent on the rhizosphere volume and microorganism biomass (Coleman et al. 1983). Both these factors are limited by access to simple carbohydrate energy (Curl and Truelove 1986). Healthy grass plants produce double the quantity of leaf biomass (Crider 1955; Coyne et al. 1995), capture and fix large amounts of carbon during photosynthesis, and produce carbohydrates in quantities greater than the amount required for normal growth and maintenance (Coyne et al. 1995). Partial defoliation of grass tillers at the vegetative phenological growth stages by large grazing graminivores causes significant quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). As a consequence the biomass and activity of microorganisms also increase (Anderson et al. 1981; Curl and Truelove 1986; Whipps 1990), resulting in greater biogeochemical cycling of essential elements (Coleman et al. 1983; Biondini et al. 1988; Klein et al. 1988; Burrows and Pfleger 2002; Rillig et al. 2002; Bird et al. 2002; Driver et al. 2005).

5 Grazing graminivores

Graminivores which graze grasslands obtain energy, protein, and macro- and micro-minerals from the forage they consume. Perennial grass leaf material consists of digestible nutrients and non-digestible structural components. The available nutritional quality of

the pre-grazed lead tillers of native cool and warm season grasses is closely related to the phenological stages of growth and development, which are triggered primarily by day length (Roberts 1939; Dahl 1995). In the northern hemisphere daylight hours increase during the growing season between mid-April and 21 June and then decrease. All native cool and warm season grasses provide adequate levels of energy to grazing graminivores throughout the growing season. However, providing adequate quantities of crude protein to grazing graminivores during the entire growing season is not as simple and requires detailed knowledge of grass tiller growth stage development and of the resulting changes in their nutritional quality curves in order to properly manipulate the grass lead tillers at specific vegetative growth stages. The crude protein concentration of grass forage available to grazing graminivores on grasslands in the North American Northern Plains is above 9.6% in the lead tillers of the cool and warm season grasses during mid-May to late July. Upland sedges have crude protein levels above 9.6% during early May to mid-July. The secondary tillers of cool and warm season grasses have crude protein levels above 9.6% during mid-July through to late September or mid-October (Whitman et al. 1951; Goetz 1963; Sedivec 1999; Manske 2000c, 2008a,c).

Grazing graminivores should be able to select a diet with adequate crude protein and energy during early June through to mid-October from the available properly manipulated forage plants. The type of animal has a strong effect on the efficiency of nutrient extraction from grazed herbage. Thus, about 15% of the nutrients contained in the consumed leaf material is extracted by stocker heifers and steers and retained for growth. About 30% of the nutrients is extracted by lactating cows, with a portion retained by the cow for production, and the remainder of the extracted nutrients passed on to her calf for growth (Russelle 1992; Gibson 2009). All the non-digestible dry matter and most of the nutrients consumed by grazing livestock are deposited on the ground as manure within a couple of days. Most of the nutrients consumed and used by livestock for maintenance are thus returned to the ecosystem in the faeces and urine. None of the herbage biomass dry matter produced during a growing season is removed by livestock from the grassland ecosystem: all the essential elements contained in the below-ground biomass and the non-consumed above-ground biomass remain in the ecosystem. Thus, almost all the essential elements used in the annual production of herbage biomass and soil organism biomass are retained and recycled in the ecosystem. However, some essential elements are lost or removed from the ecosystem as output. The metabolic process of respiration in soil organisms, plants and animals results in a loss of some essential elements as carbon dioxide, water vapour and heat energy. Some essential elements are removed from the ecosystem as weight biomass produced by insects and wildlife. The essential elements transferred from grass plants to grazing animals and used for growth are removed from the ecosystem (Gibson 2009). However, properly managed annually grazed grasslands activate the internal grass physiological mechanisms and the ecosystem biogeochemical processes which enable the capture of essential elements at quantities equal to or greater than the amount lost or removed.

6 Management of grazing

Intact grasslands can function at their full biological potential by recycling adequate quantities of essential elements through the activity of soil microbes, and by replacing lost

leaf and stem biomass of grass plants through distinctive mechanisms, all of which must be activated by partial defoliation by grazing graminivores.

6.1 'Twice-over rotation' grazing

A biologically effective 'twice-over rotation' strategy has been developed which coordinates partial defoliation events with the grasses' phenological growth stages, meets the nutritional requirements of the grazing graminivores, the biological requirements of the grass plants and the rhizosphere organisms, enhances the ecosystem biogeochemical processes and activates the internal grass plant mechanisms to function at a good-as-new condition (Manske 2016). The 'twice-over rotation' grazing management strategy uses three-to-six native grassland pastures. Each pasture is grazed for two periods per growing season. The number of grazing periods is determined by the number of sets of tillers: one set of lead tillers and one set of vegetative secondary tillers per growing season. Every pasture is grazed for 7–17 days (never less or more) during the first period. This consists of the 45-day interval from 1 June to 15 July, when partial defoliation (25–33%) of grass lead tillers between the 3.5 new leaf stage and the flower stage can increase the rhizosphere organism biomass, enhance the ecosystem's biogeochemical processes and activate internal grass plant mechanisms (Manske 1994a), as described earlier. Manipulation of these processes and mechanisms does not occur at any other time during a growing season (Manske 1999). The number of days of the first grazing period on each pasture is the same percentage of 45 days as the percentage of the total season's grazeable forage contributed by each pasture to the complete system. The forage is measured as animal unit months (AUMs). The number of days grazed is not counted by calendar dates but by the number of 24-h periods grazed from the date and time the livestock are turned out to pasture. During the second grazing period, the 90-day interval from mid-July to mid-October when lead tillers are maturing and defoliation by grazing is only moderately beneficial, each pasture is grazed for twice the number of days as in the first period. Adequate forage nutritional quality during the second period depends on the activation of sufficient quantities of vegetative tillers during the first period. Livestock are removed from intact grassland pastures in mid-October, towards the end of the perennial grass growing season, in order to allow the carry-over tillers to store the carbohydrates and nutrients which will maintain plant mechanisms over the winter. Most of the upright vegetative tillers on grassland ecosystems during the autumn are carry-over tillers which will resume growth as lead tillers during the next growing season. Almost all grass tillers live for two growing seasons, the first season as vegetative secondary tillers and the second as lead tillers. Grazing carry-over tillers after mid-October cause the termination of a large proportion of the population, resulting in greatly reduced herbage biomass production in subsequent growing seasons (Manske 2011b). The pasture grazed first in the rotation sequence is the last pasture grazed during the previous year. The last pasture grazed had the greatest live herbage weight on 1 June of the following growing season (Manske 1999, 2011b).

7 Degradation of grasslands

Degradation of grasslands occurs from three primary causes: when management of graminivore grazing fails to adequately activate the ecosystem's biogeochemical processes

and the internal grass plant mechanisms, when partial defoliation by grazing graminivores is removed from the grassland and when greater than 50% of the grass herbage biomass is consumed by heavy or late-season grazing, or fire (Manske 2012b).

7.1 Seventy-five years of non-grazing

Ownership of much of the public domain land in the North American Northern Plains was transferred from the U.S. Government through the Homestead Act of 1862 and the Federal Railroad Land Grant Act of 1864. These laws were adjusted several times, but the lawmakers failed to address the requirements of the natural resources in semi-arid regions, causing numerous long-lasting management problems. In addition, the economic depression of 1929, the severe drought conditions of 1934 and 1936, and low agricultural commodity prices during the late 1920s and early 1930s created extreme hardships for these homesteaders. Starting in 1935, the U.S. Government was permitted to repurchase more than 405 thousand hectares of submarginal homestead land in North Dakota (Hibbard 1965; Carstensen 1968; Manske 1994b, 2008b). A 1937 law provided for the implementation of follow-up conservation and utilisation programmes and the development of improved practices of management of the repurchased grasslands. The Agriculture Resettlement Administration of U.S. Department of Agriculture (USDA) authorised the establishment of experimental range-land management laboratory areas by North Dakota Agricultural Experiment Station on the Little Missouri River Badlands (Whitman 1953). In 1936, Dr. Warren C. Whitman established four two-way range-land reference areas. These included a livestock enclosure and a similar area exposed to livestock grazing on sandy, shallow, silty and overflow ecological sites (Hanson and Whitman 1938). This ongoing long-term project monitors changes in herbage biomass production, plant species composition and soil characteristics inside the non-grazed enclosure areas and in the grazed areas. During the growing season of 2011, the effects of long-term non-grazing after 75 years were compared to the effects of moderately stocked, season-long grazing treatments, that is, 7–8 months from 1 May to 31 December, with the grazing season shortened because of inclement weather conditions during most years.

Changes in vegetation composition over time were described using the 'range condition index'. Range condition index is the per cent similarity of the per cent composition of the dry weights of major plant species and categories of minor species on a current ecological site compared to the hypothetically determined standards of the per cent composition of the dry weights of the major and minor species for that same plant community at its best biological potential. Above-ground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986) sorted in the field into domesticated grasses, cool season grasses, warm season grasses, sedges, forbs, standing dead, litter and oven dried. Plant species' basal cover was determined by the ten-pin point frame method (Cook and Stubbendieck 1986) and sorted into domesticated grasses, cool season grasses, warm season grasses, sedges, forbs and litter. The density of forbs was determined by counting individual stems of each forb species rooted inside twenty-five 0.1 m² quadrats. The density of shrubs was measured by counting the individual plants of each shrub species rooted inside twenty-five 1.0 m² quadrats. A list of the shrubs, cacti and trees present was also compiled. These procedures adequately represented the shrub component of the grazed plant communities. However, because of the great extent and quantity of woody species growing inside the enclosures, these methods greatly under-sampled the woody plants within each enclosure. The surface areas of the woody

shrub and tree map units and the non-woody grass map units were measured in area as digital data in ArcGIS by visual assessment of USDA National Agriculture Imagery Program 2009 orthoimages as displayed by Google Earth. This was conducted by the Dickinson State University, Department of Agriculture and Technical Studies. Below-ground plant root biomass was collected on the non-grazed and grazed treatments of each ecological site by two replicated soil cores 7.6 cm in diameter and 10.2 cm in depth. Rhizosphere biomass was collected by three replicated soil cores, using a humane soil beastie catcher (Manske and Urban 2012a). The fresh rhizosphere material, which included the rhizosphere organisms, the active plant roots and the adhered soil particles, was separated from matrix soil by meticulous excavation with fine hand tools. Soil mineral nitrogen, nitrate and ammonium were also measured in both treatments.

The traditional season-long management practice, that is, grazed at moderate stocking rates from early May until inclement weather or to late December, was found to be severely antagonistic to silty ecological sites of mixed grass prairie grasslands. After 75 years, the plant communities had been degraded to a range condition index of 53.6 (low good). The above-ground vegetation consisted of 6.3% standing dead and 93.7% live biomass. The peak growing season live herbage biomass was 1875.82 kg/ha, comprising 41.4% domesticated grasses, 30.3% native cool season grasses, 12.0% native warm season grasses, 8.9% upland sedges and 7.5% forbs (Table 1). The basal cover consisted of 64.3% litter and 30.1% live herbage. The live basal cover was 58.1% domesticated grasses, 10.8% native cool season grasses, 9.2% native warm season grasses, 19.0% upland sedges and 3.0% forbs (Table 2). The total forb density was 10.5 stems/0.1 m², comprising 48.9% late succession, 30.5% mid-succession and 20.6% early succession forbs. The ‘woody species present’ list identified two shrub species on the grazed area. The below-ground root biomass was 24.8 kg/m³ and the rhizosphere biomass was 138.6 kg/m³ (just 34.1% of its potential weight, 406.4 kg/m³) (Manske 2015) and the available mineral nitrogen was deficient at 14.3 mg/kg (Manske 2013) (Tables 3 and 4).

The long-term non-defoliation management practice of complete rest from grazing for several decades was also extremely antagonistic to mixed grass prairie grasslands. After 75 years of non-defoliation, the plant communities had been degraded to a range condition index of 19.1 (poor). The above-ground vegetation comprised 21.6% standing dead and 78.4% live biomass. The peak growing season live herbage biomass

Table 1 Herbage biomass (kg/ha) on nongrazed compared to grazed treatment on the silty ecological site after 75 years 1936–2011

	Grazed	Nongrazed	%Difference
Domesticated	776.06	1599.26	106.07
Cool season	567.46	113.49	–80.00
Warm season	225.39	0.80	–99.65
Upland sedge	167.04	127.08	–23.92
Forbs	139.87	167.84	20.00
Total live	1875.82	2008.47	7.07
Standing dead	125.48	553.86	341.39
Litter	630.59	2421.68	284.03

Table 2 Basal cover (%) on nongrazed compared to grazed treatment on the silty ecological site after 75 years, 1936–2011

	Grazed	Nongrazed	% Difference
Domesticated	17.45	11.65	–33.24
Cool season	3.25	0.00	–100.00
Warm season	2.75	0.00	–100.00
Upland sedge	5.70	1.15	–79.82
Forbs	0.90	2.40	166.67
Total live	30.05	15.20	–49.42
Litter	64.25	84.80	31.98

Table 3 Root and rhizosphere biomass (kg/m³) on nongrazed compared to grazed treatment on the silty ecological site after 75 years, 1936–2011

Biomass	Grazed	Nongrazed	%Difference
Root	24.82	16.73	–32.59
Rhizosphere	138.63	132.08	–4.72

Table 4 Soil available mineral nitrogen, nitrate and ammonium, (mg/kg) on nongrazed compared to grazed treatment on the silty ecological site after 75 years, 1936–2011

Mineral nitrogen	Grazed	Nongrazed	% Difference
Nitrate, NO ₃	3.37	3.07	–8.90
Ammonium, NH ₄	10.92	9.81	–10.16
NO ₃ + NH ₄	14.29	12.88	–9.87

was 2008.47 kg/ha, made up of 79.6% domesticated grasses, 5.7% native cool season grasses, 0.04% native warm season grasses, 6.3% upland sedges and 8.4% forbs (Table 1). The basal cover consisted of 84.8% litter and 15.2% live herbage. The live basal cover was 76.6% domesticated grasses, 0.0% cool and warm season grasses, 7.6% upland sedges and 15.8% forbs (Table 2). The total forb density was 12.8 stems/0.1 m², with 98.1% late succession, 1.9% mid-succession and 0.0% early succession forbs. The problem of shading eliminated early succession forbs. The ‘woody species present’ list identified nine shrubs, one cactus and two trees on the non-grazed area. The area infested with woody shrubs and trees was 53.8% of the non-grazed enclosure (Fig. 2, Table 5). The below-ground root biomass was 16.7 kg/m³, the rhizosphere biomass was 132.1 kg/m³ (only 32.5% of its potential weight) (Manske 2015) and the available mineral nitrogen was deficient at 12.9 mg/kg (Manske 2013) (Tables 3 and 4).

It can be concluded that 75 years of non-grazing caused greater degradation to the site than traditional season-long management practice. The range condition index of the plant community on the non-grazed area degraded 64.4% more than that on the grazed area. On the non-grazed area, the herbage biomass of native cool season grasses, warm



Figure 2 Silty ecological site enclosure with woody shrub and tree infested plant communities and non-woody grass plant communities in the Little Missouri River Badlands, 1936–2011.

Table 5 Woody infested shrub and tree plant communities and non-woody grass plant communities on the silty ecological site after 75 years, 1936–2011

	Total enclosure area	Non-woody grass	Woody infested shrub and tree
Hectares	5.71	2.64	3.07
Percentage		46.23	53.77

season grasses and upland sedges decreased by 80.0%, 99.7% and 23.9%, respectively, and basal cover decreased 100.0%, 100.0% and 79.8%, respectively (Tables 1 and 2). The basal cover of native grasses with long shoots and stem leaves was 1.1% on the grazed area and 0.0% on the non-grazed area (a 100.0% decrease). The basal cover of native grasses with short shoots and basal leaves was 10.7% on the grazed area and 1.2% on the non-grazed area, an 89.2% decrease in the non-grazed area. Grasses with short shoots and basal leaves protect the soil and restrict invasion of unwanted plants. Thus, the higher losses of grasses with short shoots and basal leaves provided open spaces for a greater increase of domesticated grasses in the non-grazed area. The herbage biomass of domesticated grasses increased by 106.1%, and basal cover decreased by 33.2% in the non-grazed area (Tables 1 and 2). The domesticated grass basal cover was high in both grazed and non-grazed areas of the site. On the grazed area, it was 49.6%



Figure 3 Silty ecological site, enclosure with increased woody vegetation.

greater than that on the non-grazed area. However, the domesticated grass herbage biomass in the grazed area was 51.5% less than that in the non-grazed area, indicating that the domesticated grass tillers in the grazed area were numerous but small compared to the large and robust domesticated grass tillers on the non-grazed area. The herbage biomass of forbs increased by 20.0%, basal cover increased by 166.7%, forb stem density increased by 22.1%, and the number of forb species present decreased by 56.3% in the non-grazed area (Tables 1 and 2). The number of woody shrub and tree species present increased 500.0%. Analysis of black and white aerial photographs estimated shrub cover at 5% during the mid-1930s (Smith 1988). After 75 years, the area covered by the woody plant infestation in the non-grazed enclosure had increased by 976% (Fig. 3). Standing dead herbage biomass increased by 341.4% and litter increased by 284.0% in the non-grazed area (Table 1). The total dead biomass on the non-grazed area was 48.2% greater than the total live biomass. The below-ground root biomass decreased by 32.6% in the non-grazed area and coincided with the 49.4% decrease in total live plant basal cover. The rhizosphere biomass decreased greatly in both the grazed and non-grazed areas but decreased 4.7% more in the non-grazed area (Table 3). The decrease in rhizosphere microbe biomass preceded the decrease in native grass plant composition, which was followed by the increase in domesticated grass composition. Available mineral nitrogen decreased by 9.9% more on the non-grazed area (Manske 2013) (Table 4).

In conclusion, non-defoliation management by completely resting mixed grass prairie grasslands is not a revitalising strategy. Removing graminivores from grasslands to provide rest from grazing results in decreased rhizosphere organism biomass, which in turn leads to deficiencies in mineral nitrogen and other essential elements, degradation of grassland ecosystems and the encroachment of woody shrubs, trees and domesticated grasses. From these results it is clear that grazing graminivores form an essential annual component of grassland management.

7.2 Effects of fire

Many grassland ecologists have accepted the observational concept that fire prevents the intrusion of shrubs and trees into grasslands (Weaver 1954; Humphrey 1962; Daubenmire 1974; Stoddart, Smith and Box 1975; Wright and Bailey 1982). However, the presence of fire does not prove that grasslands need or are caused by fire (Heady 1975). The existence of a shrub component in a grassland is not an ecologically beneficial relationship as shrubs and grasses are adversarial inhibitive competitors. They compete for sunlight, mineral nitrogen, other essential elements and soil water. Fire in grasslands cannot prevent the invasion of, or cause the removal of, shrubs and trees that are able to reproduce by vegetative secondary suckers (Wright and Bailey 1982; Manske 2006a,b). Almost all deciduous woody plants reproduce vegetatively, except big sagebrush (*Artemisia tridentata*) (Manske 2014e). Seedlings of trees, shrubs, weedy forbs and introduced grasses cannot become established in grasslands containing grasses with full nutrient resource uptake competitiveness (Peltzer and Kochy 2001). Intrusive seedlings can only be established after a grassland has been degraded by poor management practices. Repeated prescribed fire can modify the composition of the above-ground vegetation in degraded grasslands which have been invaded by shrubs. The composition of introduced cool season grasses may change, and early succession and weedy forbs, and shrub aerial stems decrease temporarily after four repeated prescribed fires (Manske 2007a, 2011a). However, the fundamental problems of weak nutrient resource uptake, reduced water use efficiency, non-functional compensatory physiological mechanisms, impaired vegetative reproduction by tillering and diminished biogeochemical processes will remain in the degraded grassland ecosystem following repeated fire events. None of the biological, physiological or asexual mechanisms within grass plants and none of the rhizosphere microbes or biogeochemical processes they perform are activated by fire (Manske 2007a, 2011a). Almost all of the essential elements in the above-ground herbage are volatilised when a grassland is burned, and if the soil is dry, some of the below-ground essential elements are also lost (Russelle 1992). When the losses of essential elements are greater than the quantity of captured essential elements, the result is degradation of the grassland (McGill and Cole 1981). Fire does not improve grassland ecosystems biologically or ecologically and it cannot replace the partial defoliation achieved by grazing graminivores in managing healthy and productive grassland ecosystems.

8 Initial changes of restoration

A working cattle ranch, prior to 1993, was used as a study area of degraded mixed prairie grasslands. It comprised 805 ha and was managed under traditional season-long practices based on use as forage for livestock grazed at moderate-to-heavy rates, maintaining low-production native grassland ecosystems. Management based on use for recreation and wildlife habitat changed with ownership, and cattle grazing was removed for 13 years between 1993 and 2005. This resulted in severely degraded plant communities dominated by undesirable cool season domesticated grasses, primarily Kentucky bluegrass (*Poa pratensis*), smooth brome grass (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*). A 6-year restoration project was conducted from 2006 to 2011. It described and evaluated the development of the initial changes brought about by biological restoration in degraded intact grassland ecosystems through implementation of

the previously described three-pasture 'twice-over rotation' management strategy when compared to a non-grazed control (Manske 2012c). Above-ground herbage biomass, basal cover, rhizosphere biomass, and soil mineral nitrogen, nitrate and ammonium, were measured as described earlier.

Vegetation in the control pasture changed slightly during the six years of non-grazed management. Domesticated grass herbage biomass increased by 38.5% and basal cover increased by 45.5%. Cool season grass herbage biomass increased by 61.1% and basal cover decreased by 70.8%. Warm season grass herbage increased inconsequentially by 21422.5% and basal cover increased by 1600.0%. The warm season grass on the non-grazed pasture was a small remnant colony of prairie sandreed (*Calamovilfa longifolia*) that had developed a few stems above the height of the Kentucky bluegrass mats and was able to only increase herbage biomass to 172 kg/ha and basal cover to 0.85% during six growing seasons. Upland sedge herbage biomass increased by 65.5% and basal cover decreased by 63.2%. Forb herbage biomass increased by 340.5% and basal cover increased by 300.0%. Total live herbage biomass increased by 54.9% and total live basal cover increased by 21.1%. Standing dead herbage biomass decreased by 32.6%, litter biomass increased by 14.1% and litter basal cover decreased by 3.6% (Tables 6 and 7).

The composition of vegetation in the grazed pastures improved during the six years of management. Although the native grasses increased greatly, the domesticated grasses had not yet been adequately suppressed, and therefore the grassland ecosystem cannot

Table 6 Changes in herbage biomass (kg/ha) on the nongrazed control pasture, 2006–2011

	Pretreatment	Year 3	% Difference	Year 6	% Difference
Domesticated	1886.99	1478.58	−21.64	2614.06	38.53
Cool season	39.96	108.98	172.72	64.39	61.14
Warm season	0.80	50.58	6222.50	172.18	21422.50
Upland sedge	8.00	22.72	184.00	13.24	65.50
Forbs	47.15	30.26	−35.82	207.68	340.47
Total live	1982.90	1691.12	−14.71	3071.55	54.90
Standing dead	2043.64	1040.14	−49.10	1376.50	−32.64
Litter	3120.20	2824.48	−9.48	3560.23	14.10

Table 7 Changes in basal cover (%) on the nongrazed control pasture, 2006–2011

	Pretreatment	Year 3	% Difference	Year 6	% Difference
Domesticated	10.55	11.20	6.16	15.35	45.50
Cool season	1.20	3.55	195.83	0.35	−70.83
Warm season	0.05	0.40	700.00	0.85	1600.00
Upland sedge	2.85	1.90	−33.33	1.05	−63.16
Forbs	0.05	0.10	100.00	0.20	300.00
Total live	14.70	17.15	16.67	17.80	21.09
Litter	85.20	82.85	−2.76	82.15	−3.58

be said to have fully recovered. Domesticated grass herbage biomass increased by 18.3% and basal cover increased by 99.4%. Cool season grass herbage biomass increased by 1090.5% and basal cover increased by 112.4%. Warm season grass herbage biomass increased by 388.9% and basal cover increased by 488.4%. Upland sedge herbage biomass decreased by 35.0% and basal cover increased by 25.2%. Forb herbage biomass decreased by 32.2% and forb basal cover decreased by 13.8%. Total live herbage biomass increased by 32.1% and total live basal cover increased by 67.8%. Standing dead herbage decreased by 58.0%, litter biomass decreased by 45.9% and litter basal cover decreased by 10.8% (Tables 8 and 9). At the end of the 6-year study, the comparators between the grazed and non-grazed control pastures respectively were as follows: domesticated grass herbage biomass was 46.0% less and basal cover was 55.2% less. Cool and warm season native grass herbage biomass was 168.5% greater and basal cover was 438.3% greater. Upland sedge herbage biomass was 1974.2% greater and basal cover was 809.5% greater. Forb herbage biomass was 46.0% less and forb basal cover was 150.0% greater.

An important finding of this study was the difference in response of rhizosphere weights to the different treatments. Changes in these weights in the non-grazed pasture were small and appeared to be related to changes in growing season precipitation. During years 1 to 5, the growing season precipitation changed little, and was 76.6% of the long-term mean (LTM). The mean rhizosphere weight in the non-grazed pasture remained constant over the first five years, and was 76.5 kg/m³ (18.8% of potential weight, 406.4 kg/m³). During

Table 8 Changes in herbage biomass (kg/ha) on the grazed twice-over pasture, 2006–2011

	Pretreatment	Year 3	% Difference	Year 6	% Difference
Domesticated	1194.46	348.06	−70.86	1412.59	18.26
Cool season	48.75	211.62	334.09	580.36	1090.48
Warm season	11.20	25.52	127.86	54.76	388.93
Upland sedge	422.40	299.03	−29.21	274.59	−34.99
Forbs	165.45	39.39	−76.19	112.12	−32.23
Total live	1842.26	923.62	−49.86	2434.42	32.14
Standing dead	1359.50	470.81	−65.37	570.94	−58.00
Litter	1860.61	1248.58	−32.89	1005.95	−45.93

Table 9 Changes in basal cover (%) on the grazed twice-over pasture, 2006–2011

	Pretreatment	Year 3	% Difference	Year 6	% Difference
Domesticated	3.45	4.08	18.26	6.88	99.42
Cool season	1.85	4.08	120.54	3.93	112.43
Warm season	0.43	2.73	534.88	2.53	488.37
Upland sedge	7.63	10.75	40.89	9.55	25.16
Forbs	0.58	0.40	−31.03	0.50	−13.79
Total live	13.94	22.04	58.11	23.39	67.79
Litter	85.90	78.18	−8.99	76.63	−10.79

year 6, there was a substantial increase in growing season precipitation, and consequently the rhizosphere weight in the non-grazed pasture increased to 130.6 kg/m³. Nevertheless, this was still substantially less than the potential rhizosphere weight (Table 10, Fig. 4). Rhizosphere weights in the grazed pastures were not significantly different from those in the non-grazed pasture during years 1 and 2. They increased by 33% during the third year on the grazed pastures and continued to increase at a mean rate of 30.5 kg/m³ per year

Table 10 Rhizosphere weight (kg/m³) for the nongrazed control pasture and grazed twice-over pastures, 2006–2011

	Nongrazed pasture	Grazed pastures	% Difference
Pretreatment	52.23	77.99	49.32
Year 1	64.24	83.28	29.64
Year 2	77.82	92.22	18.50
Year 3	70.67	122.61	73.50
Year 4	82.88	140.32	69.31
Year 5	86.85	183.00	110.71
Year 6	130.56	214.34	64.17

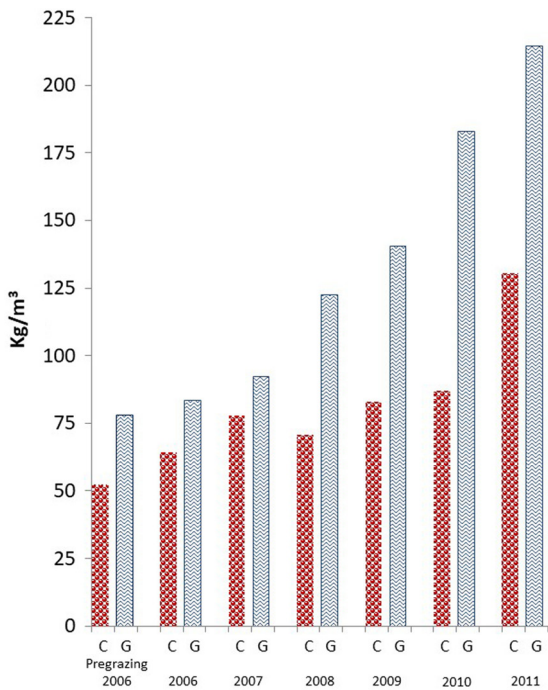


Figure 4 Rhizosphere weight kg/m³ for the control pasture (red spheres) and grazed pastures (blue waves) during six years of twice-over rotation management, 2006–2011.

from year 3 to 6, reaching a weight of 214.3 kg/m³ (52.7% of the potential rhizosphere weight) (Manske 2015) (Table 10, Fig. 4).

The quantity of mineral nitrogen available in a soil is the net difference between the total quantity of organic nitrogen mineralised by soil microorganisms and the quantity of mineral nitrogen immobilised by plants and soil microbes (Brady 1974; Legg 1975). The quantity of available mineral nitrogen varies cyclically with changes in soil temperature, soil microbe biomass, and plant phenological growth and development during the growing season (Whitman 1975). The relationships between soil microbe activity and the phenology of plant growth activity result in a dynamic cycle of available mineral nitrogen (Goetz 1975). When mineralisation activity by soil microbes is greater than plant growth activity, the quantity of available mineral nitrogen increases. When transformation (immobilisation) of mineral nitrogen by plant and soil microbe growth activity is greater than mineralisation activity, the quantity of available mineral nitrogen decreases. In this experiment, during the spring available mineral nitrate and ammonium were 64.6% and 20.5% greater in the grazed than the non-grazed treatments, respectively. Levels of total available mineral nitrogen were 111.3 kg/ha (99.4% of the threshold quantity) and 79.8 kg/ha (71.2% of the threshold quantity), that is 39.5% greater under grazing (Table 11). The rhizosphere weight was 214.3 kg/m³ vs. 130.6 kg/m³, that is 64.2% greater under grazing (Table 10). The quantity of available mineral nitrogen is also related to the rhizosphere weight. The rhizosphere microbe biomass and activity are in turn affected by the quantity of exuded short carbon compounds. The quantity of exuded carbon in the non-grazed pasture is restricted to plant leakage, while on the grazed pastures it is greater than the quantity of leakage. This is because partial defoliation by graminivores when grass tillers are at the vegetative growth stage causes greater quantities of simple

Table 11 Spring available nitrate (NO₃) and ammonium (NH₄) at incremental depths in kg/ha on silty ecological sites of the nongrazed control and grazed twice-over pastures

Soil depth (cm)	Nongrazed spring available	Twice-over spring available	% Difference
NO₃ nitrate			
0–15.2	14.84	33.19	123.65
15.2–30.5	10.92	12.75	16.76
30.5–61.0	8.61	10.64	23.58
0–61.0	34.37	56.56	64.56
NH₄ ammonium			
0–15.2	22.39	22.64	1.12
15.2–30.5	13.80	15.90	15.22
30.5–61.0	9.23	16.18	75.30
0–61.0	45.42	54.71	20.45
NO₃ + NH₄			
0–15.2	37.23	55.81	49.91
15.2–30.5	24.72	28.64	15.86
30.5–61.0	17.84	26.82	50.34
0–61.0	79.79	111.27	39.45

carbon compounds to be exuded from the grass tillers into the rhizosphere (Anderson et al. 1981; Curl and Truelove 1986; Whipps 1990; Hamilton and Frank 2001; Manske 2011b). The grazing treatment removed around 25% of the leaf material of the native grasses when the tillers were between the 3.5 new leaf stage and the flower stage. This progressively decreased the rates of leaf senescence and increased photosynthetic rates, thus increasing both the quantities of fixed carbon available for increasing plant growth and the exudation of simple carbon compounds released through the plant roots into the rhizosphere. During year 3, the rhizosphere weight in the grazed pastures increased to 73.5% greater than that in the non-grazed pasture. This in turn increased the mineralisation of greater quantities of nitrogen and other essential elements from soil organic matter, resulting in greater activity of compensatory physiological mechanisms and vegetative reproduction by tillering. The end result was an increase in herbage biomass production and basal cover of the cool and warm season grasses through year 6. Thus, restoration of degraded grasslands slowly builds the ecosystem's biogeochemical processes, and the internal grass mechanisms slowly change the plant species composition. The 3-year lag period between the start of the grazing treatment and a substantial response in rhizosphere weight, and the slow increase in above-ground herbage biomass and basal cover of the native cool and warm season grasses is important. This indicates that brief research projects which are functional for too short a time are likely to produce erroneous conclusions, for example the short-term research data reported by Sheley and Svejcar (2009) and Ranellucci et al. (2012). Traditional management practices have neglected the vital cryptobiotic microorganism component. These microorganisms are critical for the renewability of grassland natural resources. Microbes cycle essential elements from unusable organic forms into usable mineral forms. Reductions in microorganism quantity or activity therefore translate into a reduction of usable essential elements. A diminution of available essential elements is the cause of degradation in grassland productivity (Bloem et al. 2006). The quantity of essential elements used and lost from the ecosystem must be replenished at equal or greater quantities annually.

9 Future trends and conclusion

Microorganisms recycle the essential elements required for life on earth. Much of the basic science of microbe biology and processes are already known (Bloem et al. 2006). However, little of this scientific knowledge has been incorporated into the management of the world's renewable natural resources of intact grasslands, seeded grasslands, croplands, forestlands and fisheries. Productivity of these renewable resources has been declining for decades because of the reduction in the quantities of recycled essential elements (Bloem et al. 2006). Strategies are required that will enhance the capacity of microorganisms to recycle greater quantities of essential elements within the ecosystems of the renewable resources if productivity is to reach the level of future demands.

10 Where to look for further information

The key to elevating productivity on renewable natural resources, that is, intact grasslands, seeded grasslands, croplands and forestlands, is to increase the quantity of plant-available essential elements, primarily nitrogen. Mineralising greater quantities of essential elements

from soil organic matter requires a great amount of soil microbes. The increase of soil microbe biomass and activity depends on annual exudation of short carbon chain energy at quantities greater than that from plant leakage. This book chapter has shown how to increase mineralisation of essential elements with rhizosphere organisms by increasing grass exudates with partial defoliation by grazing graminivores coordinated with grass plant phenological growth stages. Additional information on this subject is available at <http://www.grazinghandbook.com>. Increasing short carbon chain energy exudates to soil microbes at greater quantities than plant leakage for the purpose of increasing available essential elements on renewable natural resources that typically do not include grazing graminivores in their standard management strategies is a major scientific challenge that will need to be solved through research in order to improve productivity that can meet future demands.

The established organisations that promote the study of grassland management are yet to make the connection between above-ground management activity and the below-ground response and the connection between the resulting below-ground activity and the above-ground plant response, primarily because of the multiple-year lag time intervals involved. The author is not aware of any organisations that actively support grazing management of grasslands in order to meet the biological requirements of grass plants and to enhance the biomass and activity of soil microbes for the purpose of improving ecosystem functionality and productivity.

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